CANON: A Canonical Composition for Building Plant Shoots From the Bottom Up

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Abstract: The phytomer concept has been useful for understanding plant development and architecture. Commonly the phytomer has been viewed as a vegetative unit consisting of a leaf, node, internode, and axillary bud, with this unit repeated within and among shoots. This definition can be extended to the inflorescence structure. Based on available knowledge and objectives, models may not fully incorporate phytomer concepts, rather some phytomers may be aggregated into a single component such as a grain component. The continuing development of object-oriented (OO) design and associated programming languages is providing opportunities for better incorporating phytomer concepts into models. For instance, the use of a Composite Pattern in an object-oriented (OO) design facilitates implementation of different scales from the phytomer to a mixture of single and aggregated phytomers for different plant components. The objectives of this paper are to use winter wheat (*Triticum aestivum* L.) to illustrate ① how plants build their canopies by the appearance, growth, and abortion/senescence of phytomer units, and ② present a conceptual prototype for translating this botanical abstraction into an OO design of a plant model, CANON, so called because the interplay of repeating phytomers is analogous to the repeating melodies of a musical composition called a canon.

In CANON OO design, the canopy is built by the addition of phytomer units that have a consistent type of communication with adjoining phytomers. This communication matches the OO structural composite design pattern described, where objects are represented in part-whole hierarchies by tree structures, with uniform treatment of individual objects and compositions of objects. At any point, the following sub-hierarchy is viewed as a single entity thus allowing parts of the hierarchy to be replaced with a single object, without affecting the preceding part of the hierarchy. This approach allows specification of sub-models of different levels of detail which could be selected at implementation or run-time. Initial implementation of the proof-of-concept using winter wheat (*Triticum aestivum* L.) vegetative phytomers is presented.

Keywords: organ development, *Triticum aestivum* L., wheat, phytomer, phyllochron, canopy architecture, object-oriented design, object-oriented phytomer model, CANON, phytomer composite pattern, scaling

1 Introduction

When Grey presented the concept of the phytomer in 1879, he presented a concept that has proven to be a useful botanical abstraction for providing a foundation to understand plant development and architecture. In this conceptualization of canopy development, canopies are built by the addition, growth, and abortion/senescence of basic building blocks (i.e., phytomers) that is repeated within and among all shoots on a plant.

Plant simulation models have varied considerably in their conceptualisation and approach for modeling plant canopy development and architecture. Extensive developmental knowledge and building canopies by phytomer units for some species such as wheat has been known from the earliest days of crop simulation modeling. However because of limited knowledge or due to the objectives of the model, few models have fully incorporated phytomer concepts.

Early efforts in simulating phytomer construction of plant canopies include use of L-systems and developmental-based simulation models using structured programming languages (e.g., SHOOTGRO, McMaster et al., 1992; Wilhelm et al., 1993; Rickman et al., 1996). More recent work on functional-structural modeling (e.g. Vos et al., 2007) has provided considerable detail on phytomer construction of canopies.

Many initial efforts at object-oriented (OO) design of plant growth models did not reflect how the plant canopy actually develops by phytomer units. A common approach was to view the plant from the concept that it consists of leaf, stem, root, and seed components (e.g., APSIM, McCown et al., 1996; APSIM-Plant, Wang et al., 2002; Sequeira et al., 1991; 1997). In this design, the phytomer unit components are split into these generic plant components. With advances in OO design and application of OO Design Pattern, new possibilities for capturing botanical knowledge of the phytomer into simulation models is possible. The Composite Design Pattern has not received much recognition in many OO designs for crop simulation models. This design pattern can be utilized for plant models based on phytomer concepts so that the phytomer concepts can be aggregated into lower levels of resolution (such as entire shoots or inflorescences) or different conceptualizations of the plant such as mentioned above.

The objectives of this paper are to use winter wheat as a case study to ① discuss how plants build their canopies by the appearance, growth, and abortion/senescence of phytomer units and extend the phytomer concept into the inflorescence, and ② translate this botanical abstraction into an OO design based on the Composite Design Pattern and provide initial implementation efforts (CANON).

2 Phytomer Unit and Building Plant Canopies

While various definitions of phytomers have been proposed (Wilhelm and McMaster, 1995), most commonly the phytomer is viewed as a unit consisting of a leaf, node, internode, and axillary bud, with this unit being repeated within and among shoots (Fig. 1). This basic definition has been extended to include the nodal root buds (Klepper et al., 1984), and is considered a "vegetative" phytomer. The plant builds its canopy by the addition, growth, and abortion/senescence of these vegetative phytomer units on a shoot, with the same process for each shoot (Rickman and Klepper, 1995). The vegetative phytomer unit concept can be extended for building the spike inflorescence using "reproductive" phytomers, where both the spikelet and floret parts of the wheat inflorescence have analogs to the vegetative phytomer leaf and axillary buds. The main axis of the wheat spike (i.e. the rachis) is built by the sequential addition of phytomers consisting of spikelets (=leaf), with the other similar phytomer components of the node, internode, and axillary bud. In turn, the main axis of each spikelet (i.e., the rachilla) is built by the sequential addition of phytomers consisting of florets (=leaf), and the node, internode, and axillary bud. Others have recognized this pattern of repeated phytomers for barley (*Hordeum vulgare* L.). For instance, Bossinger et al (1992) described a phytomer concept for barley including spikelet components, roots, tillers and branches which Forster et al. (2007) extended to all elements of the barley plant. The resulting model was entirely composed of phytomers to describe the whole canopy architecture. This dynamic interplay of phytomers within and among plant components can be viewed as analogous to a composition of music called a canon (a familiar simple form being a round) where individual phytomers repeat a part against and with other phytomers as do the melodies of a canon. This analogy led to the naming of our proof-of-concept OO design as CANON.

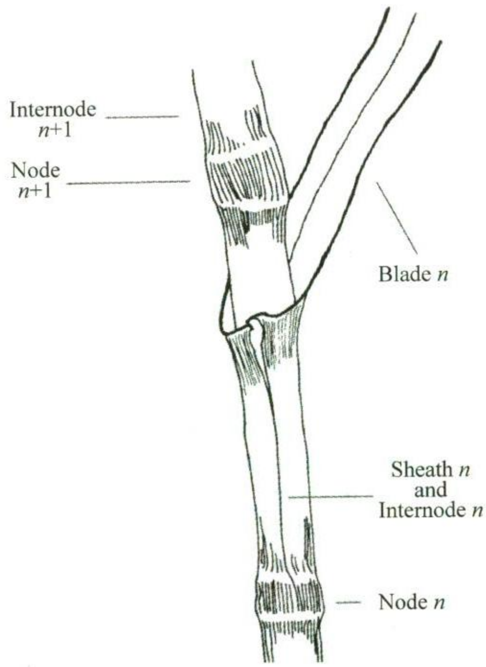

Figure 1 Common definition of a vegetative phytomer unit (From McMaster et al., 1991)

Considerable data are available for certain species, particularly wheat, to quantify the orderly development of the plant canopy by the dynamic interplay of phytomers. Using wheat as a case study, each vegetative phytomer can be considered to be initiated when either the leaf primordium is formed on the shoot apex or when the leaf primordium further differentiates and grows resulting in the appearance of the leaf. Since the primordia and leaves are produced sequentially with a fairly consistent pattern related to thermal time (Rickman and Klepper, 1995; McMaster, 2005), the production of vegetative phytomers on a shoot is quite predictable. In a similar manner, the production of each spikelet primordium on the rachis of the spike is analogous to the production of vegetative phytomers, and generally is 2 to 3 times faster than the rate of leaf primordia production (Hay and Kirby, 1991; Kirby, 1974). On the axis of the spikelet, floret primordia production is also quite consistent with thermal time. Therefore, the general concept of building a canopy by the addition of phytomers within a shoot can be quantified for winter wheat. The timing of new axes, or shoots, can be well related to thermal time, and has been successfully correlated with main stem leaf number (Klepper et al., 1982; 1984). Therefore, the building of an entire wheat canopy by the addition of phytomers has been quantified by numerous scientists (e.g. Rickman and Klepper, 1995).

A similar understanding of the orderliness and predictability of the growth of each component of the phytomer has been developed over time. For instance, an increase in leaf dimensions and biomass of successive leaves on a shoot has been studied (Hay and Wilson, 1982). The internode component of the first few vegetative phytomers is negligible, and appreciable internode elongation does not begin until shortly before the developmental stage of jointing. As with leaves, successive internodes of vegetative phytomers increase in length (McMaster et al., 1991). Kernel growth normally follows a sigmoidal pattern, and a common pattern of final kernel size tends to be observed within the inflorescence ((McMaster, 1997) cites many references).

Similarly, considerable knowledge of the senescence or abortion of phytomer components is available, such as numerous studies of tiller and kernel abortion cited in McMaster (1997). Of critical importance is predicting the timing of developmental events, or phenology, necessary to simulate the state of each phytomer and phytomer component. Wheat phenology has been successfully simulated in many crop simulation models such as APSIM (Keating et al., 2003), ARCWHEAT1/2 (Porter, 1984; 1993; Weir et al., 1984), Sirius (Jamieson et al., 1995; 1998), and DSSAT (Ritchie and Otter, 1985; Ritchie, 1991; Hunt and Pararajasingham, 1995; Jones et al., 2003; Hoogenboom et al., 2004).

3 Translation of Phytomer Concept into OO Design

With the botanical conceptualization of a phytomer as a starting point, the fundamental components of a phytomer unit were identified for our OO design. In summary, for our proof-of-concept purposes, a plant consists of two basic types of components each built using phytomer units. One component is a vegetative component consisting of stems or axes with leaves and internodes and the other a reproductive component (a spike) consisting of axes with spikelets and internodes. A vegetative phytomer has components which, for our proof-of-concept purposes, are a leaf, an internode, an axillary axis and a root while a reproductive phytomer has components of spikelet, internode and axillary axis. Phytomers are arranged in sequence to form an axis (a generic term we use in the prototype for a culm or tiller or shoot).

A phytomer can be described in terms of its properties (e.g. its component parts such as leaf, internode, axillary axis, root, its state such as growing, senescing, its age, etc.), processes (e.g. growth and senescence, ageing and change of state) and messages to its adjoining phytomers and its own components (e.g. collecting information such as leaf area of all leaves along the hierarchy from this phytomer, or signalling a whole plant event such as death). This description can be viewed in OO terms as an object that has data (properties), methods (processes) and a consistent interface for the passing of messages to other phytomer objects and its own component part objects (e.g. communication by signalling and movement of resources). A series of recursive and like phytomers form a plant component such as a vegetative axis, with the phytomer properties describing their type and function. To form a different type of component such as a reproductive spike of phytomers or an aggregate axis (reproductive or vegetative), the phytomers or their aggregate change to a new set of properties describing their new functionality. Thus a plant component can be viewed as either a composite set of recursive phytomers or as an aggregation of phytomers into a single plant component. Many functional-structural models are based on this conceptualization, using a phytomer approach for vegetative (culm and canopy) development and an aggregated organ approach for root and reproductive (grain) development (Vos et al., 2007). Tomlinson et al (2007) use this approach for clonal bunchgrasses.

In this model, a phytomer has a consistent type of communication with adjoining phytomers, regardless of the hierarchical structure that follows. This matches the object-oriented, structural composite design pattern described by Gamma et al. (1994), where objects are composed into tree structures to represent part-whole hierarchies, in which individual objects and compositions of objects are treated uniformly by each preceding object in the hierarchy (parent object). At any point in the tree structure of a composite pattern, the following sub-hierarchy is treated as a single entity. This enables parts of the hierarchy to be replaced with a single simple aggregated object, without affecting the preceding part of the hierarchy. For example, the phytomeric inflorescence sub-hierarchy of the structure could be replaced with a simpler sub-hierarchy or a single object. This replacement strategy can be used for any logical group in the hierarchy. This approach allows specification of sub-models of different levels of detail which can be selected at run-time, without altering the object design.

The phytomer model we use is a modification of the common vegetative model of leaf+sheath, node+internode, and axillary bud (Fig. 1) by the addition of a root bud and extending the model to describe the reproductive structure (Fig. 2).

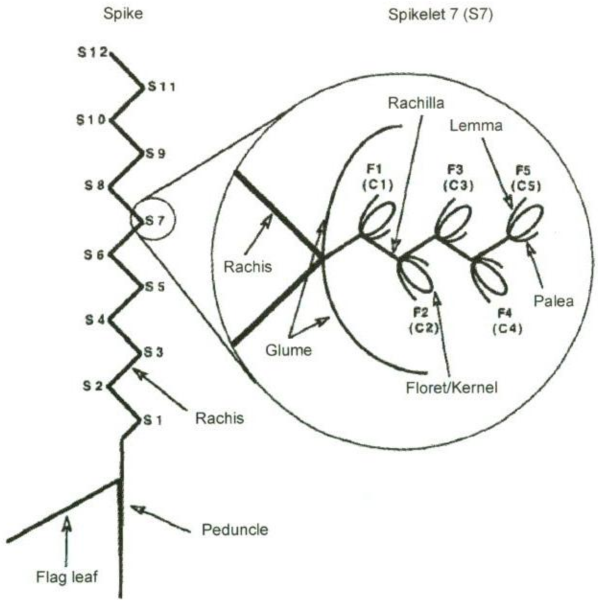

Figure 2 Reproductive phytomers consisting of spikelets (=leaf) on the main axis (=rachis) and florets (=leaf) on spikelet axis (=rachilla) (From Wilhelm and McMaster, 1996)

This model is extended further by Forster et al. (2007) who describe every organ in terms of a basic phytomer unit. Complex plant growth and development models are commonly built out of simple specialised plant components. A simple implementation could define OO classes for simple structures such as grain, stem, leaf and root. This approach does not consider the biological significance of the phytomer as a building block of plant growth and development. A phytomer approach to modeling plant architecture produces a botanical abstraction of a phytomer in an object-oriented (OO) design. Commonly, phytomers are incorporated into a model design by defining the phytomer as a class with a stem class acting as a container class for all the stem phytomers, keeping inflorescence (grain), leaf and root as simple classes (Fig. 3). In turn the main stem and each tiller could be defined as larger container classes for the leaf, stem, grain and root, and the whole plant in turn defined as a still larger container class for the main stem and tillers, similar to the functional-structural model of Tomlinson et al. (2007).

To implement the approach described by Forster et al. (2007), phytomers build each component of the plant, so different classes could be defined for the phytomers in each organ. Container classes would then be defined for all phytomers of each type and so on as described before.

Gamma et al. (1994) point out that the problem with this approach is that client code that uses these classes has to treat the simple and container classes differently, even though each can have the same basic properties and processes. To overcome this, they define a Composite Design Pattern (Fig. 4) which describes how to use recursive composition so that the client code doesn't need to make a distinction between simple and container classes and treats all objects in the composite structure uniformly. Thus a simple object has no children, while a composite object has children which could be simple or composite objects.

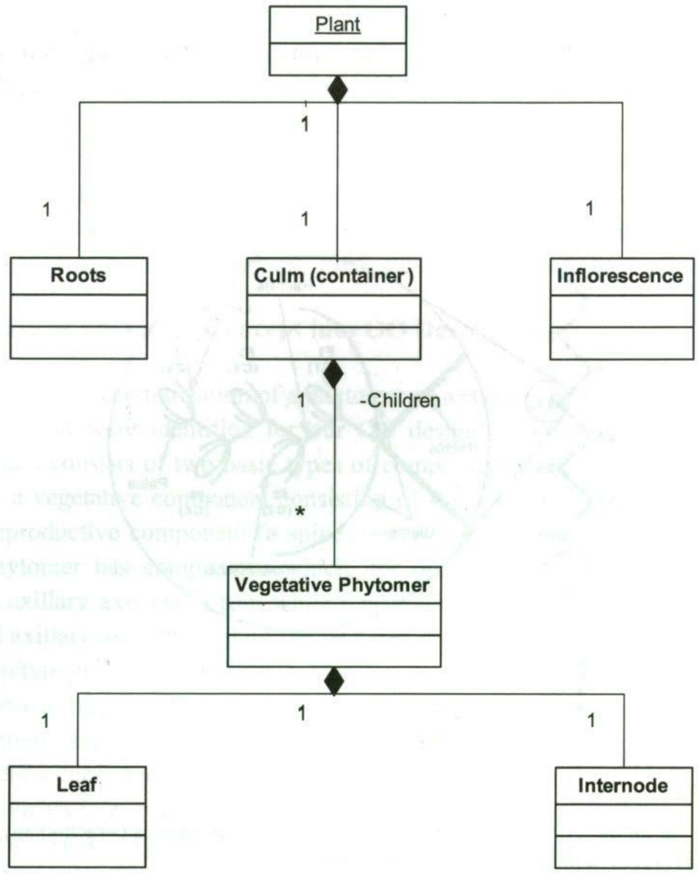

Figure 3 A basic phytomer model with a culm containing vegetative phytomers consisting of a leaf and internode, and simple components for the roots and reproductive inflorescence

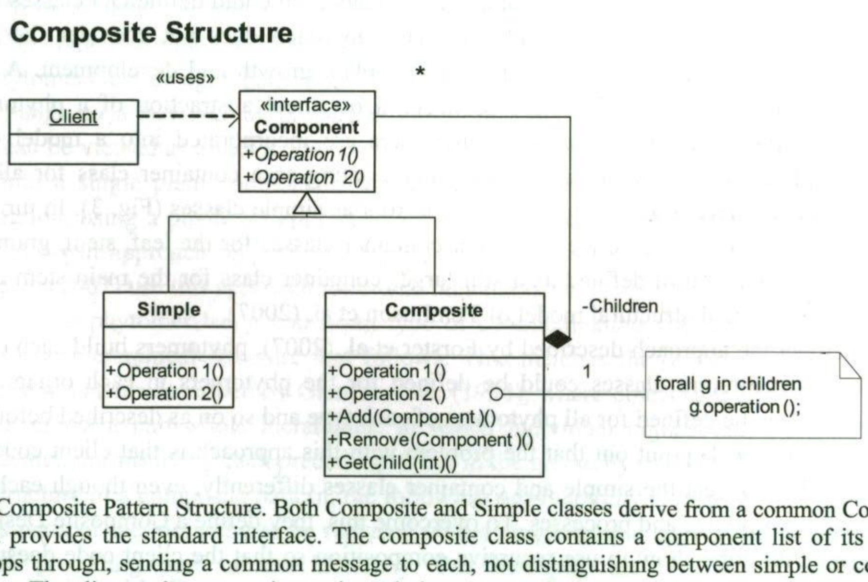

Figure 4 Composite Pattern Structure. Both Composite and Simple classes derive from a common Component class which provides the standard interface. The composite class contains a component list of its children which it loops through, sending a common message to each, not distinguishing between simple or composite class children. The client code communicates through the common Component class, again not distinguishing between simple or composite classes. A Simple class is a Component and Composite class is a Component. A Composite class also has a Component (one or more) which are its children

Figure 5 shows the simplicity of a basic composite phytomer plant model matching that of Forster et al. (2007). This can be extended to match other phytomer models as described by Bossinger et al. (1992), Tomlinson et al. (2007) and in this paper, so a "simple phytomer" class could represent either a phytomer or an aggregate component such as the spike.

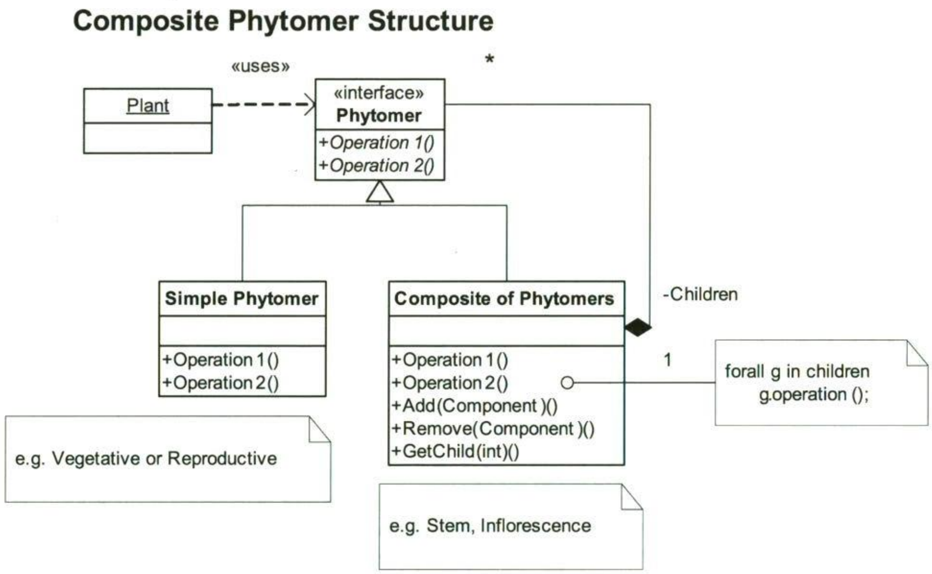

Figure 5 Composite Phytomer Model. Plant is the client that communicates with the phytomer hierarchy through the Phytomer class which provides a standard interface to all components in the hierarchy. A simple phytomer represents a single phytomer, either vegetative or reproductive, or an aggregation of phytomers into a single component. A composite of phytomers represents a collection of phytomers such as a stem (axis) or inflorescence (spike)

4 Initial Implementation Efforts of OO Design

Proof-of-Concept Development

While these concepts could apply to any species, we have chosen to implement the design using winter wheat (*Triticum aestivum* L.) because information for this species is readily at hand and it is conceptually very simple. For proof-of-concept simplicity, our initial implementation is constrained to the vegetative phytomers (not including nodal roots). Figure 6 shows the class diagram of this initial implementation. In the next development phase, we will introduce reproductive phytomers.

We are beginning the implementation of our OO design into a proof-of-concept (CANON) using the C++ programming language. In this implementation, we are initiating phytomers, growing phytomer sub-components, senescing phytomer components, and repeating this process for new axes, or shoots. Many of the rules for the methods are being derived from the SHOOTGRO model (McMaster et al., 1992) and using winter wheat as the model plant. As a proof-of-concept we are assuming optimal growing conditions (McMaster et al., 1991; 1992; Wilhelm et al., 1993). Initial tests are showing the OO design principles outlined in this chapter are able to be implemented into a plant growth simulation model. There are a number of alternative implementations of the phytomer design. A phytomer, upon creation, could be populated with dormant buds for all of its components, which can then be activated by nominated events. In our implementation, we have chosen not to form an axillary bud, but initiate a new axillary axis when the bud begins to elongate, which is signaled by a phenological event. Similarly, we do not form a node and initiate the internode when its elongation begins.

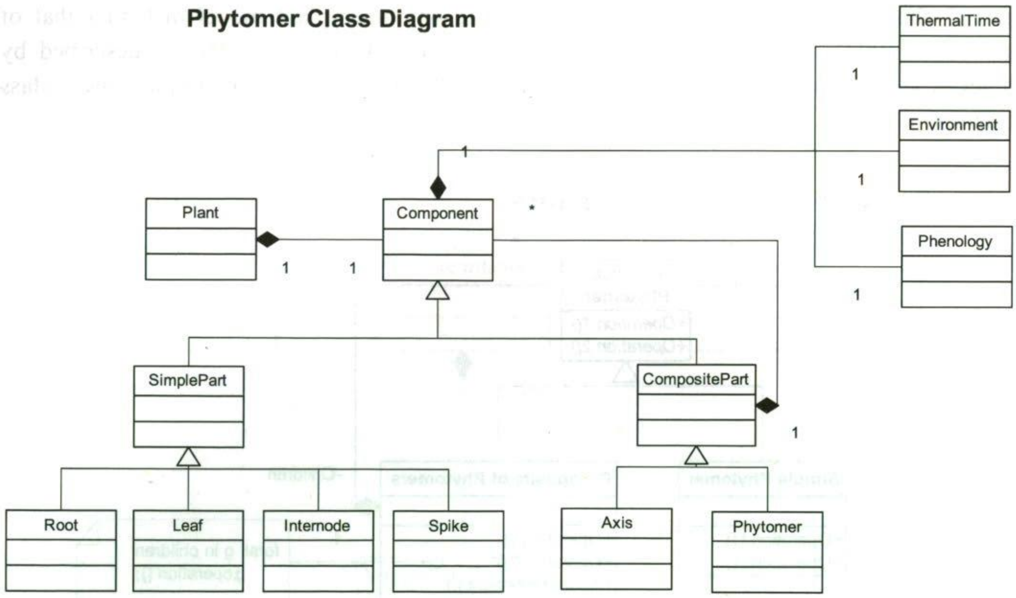

Figure 6 Class diagram of CANON phytomer model. This shows the prototype class relationship structure of vegetative phytomers with their components (root, axis, internode and leaf). Here each Root, Leaf, Spike and Internode class is a SimplePart, each Axis and Phytomer is a CompositePart, each SinglePart and CompositePart is a Component and Plant has a Component. CompositePart also has one or more Components. The Component class has service classes for thermal time, environment (weather) and phenology which are inherited for use by all its sub-classes

Figure 7 shows our implementation of phytomers on a wheat plant with a main stem, primary tiller (T1), and spikelet/reproductive phytomers. The internode of each phytomer is developed while the other buds are suppressed or developed. Along the main axis or stem, the root bud of Phytomer 0 is developed while the leaf and axillary buds are suppressed. The next phytomer to develop on the main axis, Phytomer 1, has the root bud suppressed with the leaf developed and axillary bud developed into a secondary axis or branch. Phytomer 1 is followed by vegetative phytomers until the terminal phytomer which suppresses the leaf and develops its axillary bud into an axis of reproductive phytomers in which the reproductive organ is developed and the leaf and root buds suppressed. The secondary vegetative axes begin with a Phytomer 0 consisting solely of an internode and develop similarly to the main axis.

5 Discussion

The Conundrum—Multiple and Variable Scales

Limited knowledge and application objectives determine the levels of detail or scale used within a model. For example, a model may be built with three simple components viz. vegetative, reproductive and root, to meet a project's simulation requirements. As knowledge improves and objectives change, the vegetative component may be developed to a more detailed sub-model constructed with phytomers, while light capture by the canopy may be adequately simulated at the whole plant level. This illustrates simulation at three scales within the model, with leaf growth and development at phytomer levels (detailed phytomer level), with leaf area being aggregated at plant canopy level for light interception (whole of plant level), while the reproductive spike is simulated as a single grain component (aggregated organ level). Another application may need the spike component

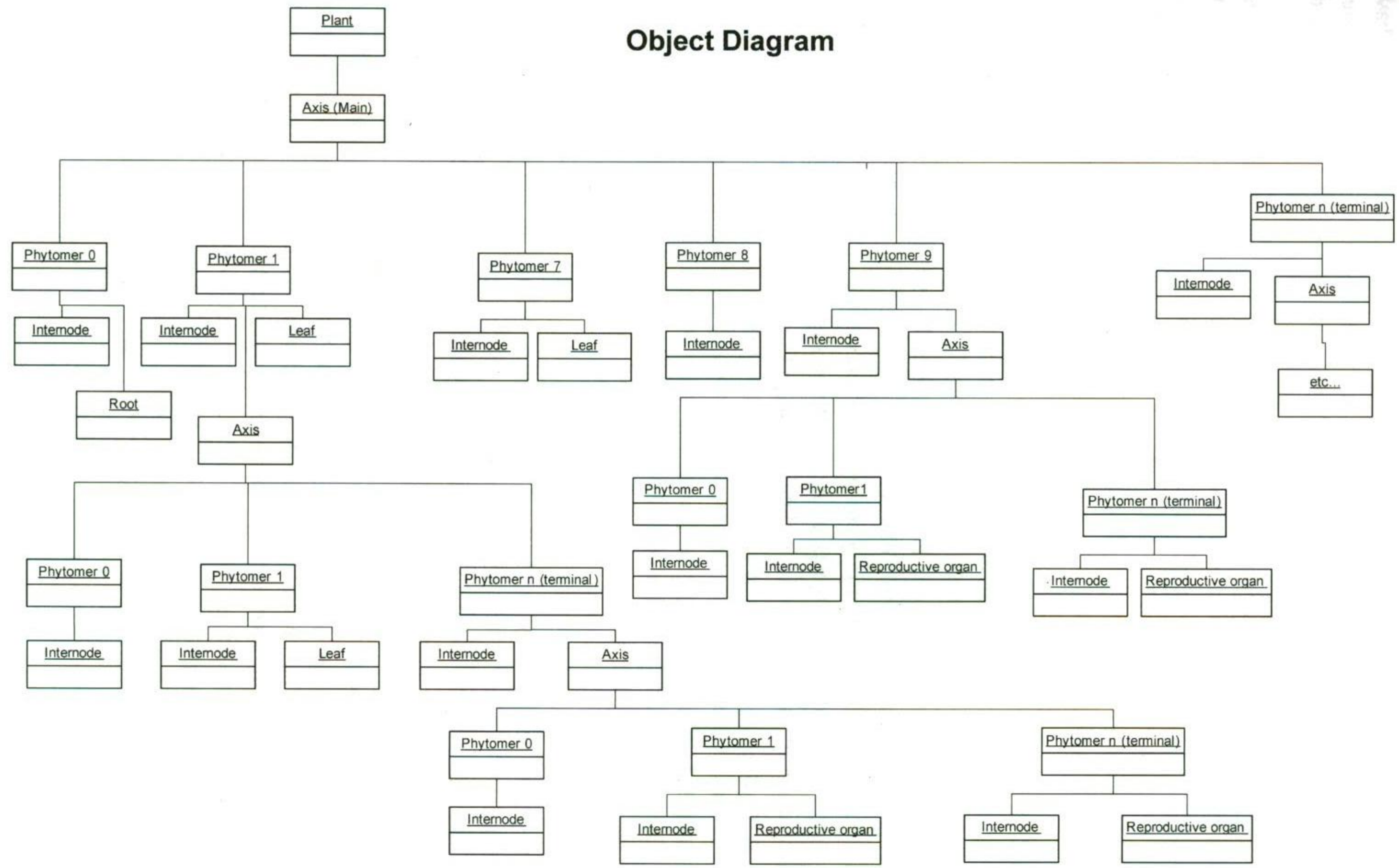

Figure 7 Object diagram of CANON phytomer model. This demonstrates a potential structure of vegetative and reproductive phytomer objects with their components (root, axis, internode, leaf and grain)

to be simulated at phytomer levels. The challenge is to facilitate the incorporation of multiple levels of scale into a model with runtime selection of these scales while providing for the addition of new expanded or reduced scales as knowledge increases and application requirements change. Any change in configuration due to scales produces essentially a different model which will have associated changes in model performance and validation. In this paper, we are primarily interested in providing a simple design which facilitates easy opportunities for simulating at any level of resolution.

In summary, the requirements for our proof of concept model are: ① ability to replace a logical group of phytomers with a single component or vice versa, ② ability for some processes to operate at whole plant level, using the collective information of more detailed components and distributing new information to the more detailed components, and ③ ability of components, such as phytomers to represent different types or classes of plant components, such as vegetative and reproductive. An additional objective is for components to be respecified to represent other species.

Advantages of the Composite Design Pattern

The OO Composite Design Pattern underpins our solution to the conundrum by satisfying the three main requirements identified above that must be demonstrated in our proof of concept. There are a number of important effects the Composite Pattern has on the code. It defines hierarchies of simple objects and composite objects. The simple objects can be composed into compound or composite objects, which can be composed in turn into compound objects and so on, in a recursive manner. This enables simple and composite objects to be indistinguishable to the code that uses these objects. The advantage of this is the code is simplified as both simple and composite objects are treated alike and the code doesn't know or care if it is using a simple or composite object. The code is simplified as it doesn't need to distinguish between the types of objects (e.g. leaf or axis). A very important advantage of this behaviour is that it makes it easier to expand the hierarchy by adding new kinds of single or composite components and or to collapse sub-hierarchies into a simpler composite component or even further into a single simple component.

Application to Plant Modeling

Implementing a plant model based on the Composite Design Pattern can simplify the code and reduce the potential for errors. The recursive nature of the pattern allows indeterminate or determinate plant development to be easily implemented. Phytomers or their aggregate replacement in the hierarchy can be implemented to be self configuring, based on the phytomer or component type (e.g., vegetative or reproductive).

Depending on the type, development of phytomeric components can be switched on or off, such as the root bud. Axillary buds can be switched on to form a new tiller or secondary branch axis or left off to remain dormant. The generality of this design allows modeling at various scales as appropriate for the problem being studied. It also allows the phytomer model to be applied to other monocots and dicots as described in McSteen and Leyser (2005) by re-specification of the phytomer and component parameters.

OO plant simulation models that have leaf, stem, grain and root objects (e.g. APSIM-Plant, Wang et al., 2002) could be adapted to this design which would then provide the flexibilities described earlier.

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